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Fruit nutritional composition and non-nutritive traits of indigenous South African tree species

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Abstract

Frugivorous animals play a major role in dispersing tropical, and to a lesser extent, temperate tree species. In order to attract potential seed dispersers, plants generally offer a reward of fleshy fruit pulp. Criteria for fruit choice by avian frugivores are influenced by a number of non-nutritive (e.g. fruit size and colour) factors; and nutritional composition of the fruit. There is a paucity of nutritional composition and other fruit trait data of indigenous South African fruit. This information is necessary in order to determine which frugivores are likely to ingest which fruits and consequently act as potential seed dispersal agents. This information would provide us with an understanding of the inter-relationships between indigenous fruit and frugivores in South Africa. Consequently nutritional composition was investigated in various indigenous fruit species that avian frugivores feed on. Fruits were collected from 38 indigenous tree species found in KwaZulu-Natal Afromontane and coastal forests. Pulp was freeze-dried to constant mass and then analysed for sugar, lipid and protein content; and for water content determination. Fruit width in this study ranged from 4 mm (*Searsia rehmanniana* and *Trema orientalis*) to 40 mm (*Annona senegalensis*, *Ficus sur* and *Xylotheca kraussiana*). Of the fruits examined in this study 29% were black and 43% were red when ripe. Most (84%) fruit species analysed for sugar content were hexose dominant with 50% being fructose and 34% being glucose dominant. Only 16% of the fruit species analysed were sucrose dominant. Fruits in this study were generally observed to be high (mean: 68.1 ± 3.3%; n = 30) in water content; and low in protein and lipid content respectively (mean: 8.2 ± 0.5%; 9.3 ± 2.2%; n = 30) indicating that these fruit species could be considered as nutrient-dilute. Future studies need to determine the nutritional composition of the remaining indigenous South African fruit in order to develop a comprehensive database as well as examining non-nutritive factors.

Keywords: Fruit colour; Fruit size; Fruit sugars; Indigenous fruit; Lipids; Protein

1. Introduction

A large proportion of South Africa's biodiversity is supported by indigenous forests (Mucina and Rutherford, 2006). However indigenous forest is the smallest biome found in South Africa and this biome has become severely fragmented due to anthropogenic activities (Chapman et al., 2006; Cooper, 1985; Eeley et al., 1999; Geldenhuys, 1989; Lawes et al., 2000; Low and Rebello, 1996). Fragmentation is likely to negatively affect the forest flora as well as the fauna with which these plants interact (Chapman et al., 2006; Cooper, 1985; Geldenhuys, 1989; Lawes et al., 2000; Low and Rebello, 1996). It is thus essential that we gain an understanding of the mechanisms that govern plant–animal interactions in forest ecosystems in order to develop management plans for forest conservation (Kirika et al., 2008).

Dispersal of seeds is essential in maintaining and renewing plant communities (Chave et al., 2002; Herrera, 2003; Howe and Smallwood, 1982). Frugivorous animals play a role in dispersing up to 90% of tropical and between 30 and 50% of temperate tree species (Herrera, 2003; Howe and Smallwood, 1982). In order to attract potential seed dispersers, plants offer a reward of fleshy fruit pulp (Howe, 1986).

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Criteria for fruit choice by avian frugivores may be influenced by a number of non-nutritive factors such as fruit colour, size, and secondary compounds (Jordano, 2000; Murphy, 1994; Sallabanks, 1993; Wheelwright, 1985). Width of avian frugivores' gape limits the size of the fruit that can be ingested intact (Jordano, 2000; Martin, 1985; Wheelwright, 1985) although feeding behaviour may further influence this as some birds are 'gulpers' meaning that they swallow their fruit whole and therefore cannot ingest fruits larger than the width of their gape (Levey, 1987; Symes and Downs, 2001).

Birds usually consume black or red fruits (Burns, 2005; Ridley, 1930; Willson et al., 1989) although fruit colour as assessed by humans is likely to be different to fruit colour assessed by birds (Schaefer et al., 2006). Bird's eyes are well adapted to see red colours as their retinas contain four cone types (Bowmaker, 1998; Jacobs and Deegan, 1999).

Bird's digestive ability and fruit's nutritional value are considered to be the most important factors that influence fruit choice (Fuentes, 1994; Izhaki, 1992; Johnson et al., 1985; Martínez del Rio and Restrepo, 1993; Worthington, 1989). Sugar types and concentrations in nectar have recently been explained by the plants' associations with either specialist or generalist nectar-feeding birds (Brown et al., 2010a,b; Johnson and Nicolson, 2008). The sugars and sugar concentrations found in fruits, however, are not so easily explained and have traditionally been classified according to a dichotomy of high investment fruits (nutrient-dense) and low investment (nutrient-dilute) fruits although it has been suggested that fruits instead appear to be arranged along a continuum of nutrient values (Howe and Estabrook, 1977; Howe and Smallwood, 1982; Izhaki, 1993; McKey, 1975). Nutrient-dense fruits are considered to be variable in protein, relatively high in lipids, and low in water and carbohydrates (Izhaki, 1993). Conversely, nutrient-dilute fruits are considered to be low in fibre and protein, high in water, and have fewer carbohydrates than nutrient-dense fruits (Herrera, 1982; Izhaki, 1993; Snow, 1981).

Fruit pulp varies in both sugar composition and concentration (Martínez del Rio and Stevens, 1989). Fruit pulp consists of three main sugars; the disaccharide sucrose and the hexose monosaccharides glucose and fructose (Baker et al., 1998; Lotz and Schondube, 2006). The ability of the avian frugivores to efficiently digest the different sugars may affect fruit choice (Avery et al., 1999) and several studies have shown that some bird species (e.g. some families from the Sturnid-Muscicapid lineage) avoid sucrose-rich fruits as they lack the enzyme sucrase and are therefore unable to efficiently digest sucrose (Levey and Martínez del Rio, 2001; Martínez del Rio, 1990; Martínez del Rio and Restrepo, 1993; Schuler, 1983). Even those birds that do possess sucrase may prefer hexose sugars in choice tests as they may not be able to digest sucrose efficiently enough (Avery et al., 1995; Martínez del Rio et al., 1992). Birds may also prefer glucose and fructose sugars over sucrose as their fast gut passage rates prevent sucrose from being hydrolysed and absorbed efficiently (Karasov and Levey, 1990; Martínez del Rio and Restrepo, 1993).

As there is a paucity of data on the nutritional composition and other fruit traits of indigenous South African fruits (but see Gaynor, 1994; Lawes, 1990; Voigt et al., 2004; Wirminghaus et al., 2002) we are uncertain whether South African fruits follow similar trends observed in studies done in other parts of the world. This information is necessary in order to determine potential seed dispersal agents. This information would provide us with an understanding of the inter-relationships between indigenous fruit and frugivores in South Africa. Consequently nutritional composition and other non-nutritive traits (e.g. fruit colour and size) were investigated in 38 indigenous fruit species.

2. Materials and methods

2.1. Collection

Ripe fruits were collected during 2010 from a range of indigenous tree species (n = 38) (Table 1) found in KwaZulu-Natal Afromontane and coastal forests. Fruits that were collected from the same region in KZN were pooled in order to obtain enough fruit pulp for the analyses. Fruits were frozen (c. −18 °C) immediately after collection until they could be freeze-dried. Pulp was freeze-dried to constant mass and water content determined, and then milled to a powder for nutritional composition analyses. Data on fruit size and colour were obtained from Griffiths and Lawes (2006) and Boon (2010).

2.2. Fruit sugars

Sugar concentrations were determined according to Liu et al. (1999). Freeze-dried material (0.05 to 0.10 g) was mixed with 10 mL 80% (v/v) ethanol and homogenised for 1 min. Thereafter, the mixture was incubated in an 80 °C water bath for 60 min to extract the soluble sugars. Subsequently the mixture was kept at 4 °C overnight. After centrifugation at 12,000 *g* for 15 min at 4 °C, the supernatant was filtered through glass wool and taken to dryness in a vacuum concentrator. Dried samples were resuspended in 2 mL ultra-pure water, filtered through a 0.45 μm nylon filter and analysed using an isocratic HPLC system (LC-20AT; Shimadzu Corp., Kyoto, Japan) equipped with a refractive index detector (RID-10A; Shimadzu Corp.) and a 300 mm–7.8 mm Rezex RCM-Monosaccharide column (8 μm pore size; Phenomenex®, Torrance, CA, USA). Concentration of individual sugars in fruits was then determined by comparison with authentic sugar standards (sucrose, glucose and fructose standards extracted from fruit; purchased from SIGMA with a purity minimum of 99%).

2.3. Fruit lipids and proteins

Fruit lipids were extracted using a Buchi 810 Soxhlet fat extractor (according to the Soxhlet procedure). Fat was extracted from the sample by the solvent petroleum ether and percentage fat was calculated based on the gravimetric analysis (AOAC Official Method 920.39). Fruit protein was analysed in a LECO Truspec Nitrogen Analyser using the Dumas Combustion method (AOAC Official Method 990.03). Two assumptions were made in calculating protein content based on

Table 1
Fruit characteristics of indigenous tree species used in the study.

Tree species	[a]Colour when ripe	[a]Fruit size	Fruit mass (g)	Sucrose (mg/g)	Glucose (mg/g)	Fructose (mg/g)	Sucrose : hexose ratio	% water content	% protein content	% lipid content
Annona senegalensis	Yellowish-orange	50×40 mm	25.07±0.73 (8)	5.93	36.49	43.75	1:13.54	68.21	8.88	10.00
Antidesma venosum	Purplish-black	7×5 mm	0.08±0.007 (10)	2.13	28.55	34.53	1:29.55	63.61	7.85	6.33
Apodytes dimidiata	Black/red	8 mm	0.30±0.017 (10)	4.25	13.55	8.81	1:5.26	58.99	8.02	27.66
Bridelia micrantha	Black	10×7 mm	0.40±0.02 (10)	2.14	33.51	40.13	1:34.34	70.84	7.58	2.25
Canthium inerme	Brown	15×10 mm	0.90±0.10 (10)	4.01	53.49	58.81	1:28.02	58.46	7.10	6.10
Carissa macrocarpa	Red	50×30 mm	14.23±1.32 (10)	13.05	56.12	59.26	1:8.84	82.54	4.41	7.25
Celtis africana	Yellow	8 mm diam	0.20±0.008 (10)	43.39	3.13	42.37	1:1.05	51.75	7.73	5.00
Clerodendrum glabrum	Yellowish-white	10 mm diam	0.61±0.05 (10)	9.79	54.98	36.52	1:9.34	81.33	8.37	3.47
Commiphora neglecta	Red	14 mm diam		1.90	0.27	0.42	1:0.36	77.46		
Cordia ovalis	Orange-red	20 mm	1.13±0.12 (10)	11.47	33.23	34.94	1:5.95	67.20	10.64	0.62
Ficus ingens	Purple	13 mm diam		0.44	3.74	3.54	1:16.52			
Ficus lutea	Yellow to brown	15–30 mm diam	3.02±0.17 (10)		44.23	32.96		82.79	5.47	2.21
Ficus natalensis	Red-brown	10–20 mm diam	0.66±0.02 (10)	2.20	22.49	20.36	1:19.44	87.12	8.32	3.40
Ficus petersii	Reddish	13 mm	4.75±0.20 (10)		60.50	46.68		81.60	5.39	2.29
Ficus sur	Pink-red with pale spots	20–40 mm diam	12.02±0.82 (10)	4.27	23.58	25.32	1:11.45	87.77	8.37	5.88
Ficus trichopoda	Red	10–20 mm diam	4.25±0.85 (10)		54.78	40.22		83.18	6.72	2.37
Grewia occidentalis	Reddish purple to brown	25 mm diam	0.75±0.10 (10)						8.53	2.58
Harpephyllum caffrum	Red	30×17 mm	4.97±0.53 (10)	61.73	12.32	6.35	1:0.30	68.50	4.75	1.42
Kraussia floribunda	Purple to black	8 mm diam	0.41±0.02 (10)						2.99	5.26
Maesa lanceolata	Cream	6 mm diam	0.07±0.004 (10)	3.35	22.15	25.57	1:14.26	83.70	12.01	11.94
Mimusops caffra	Red	25 mm diam	1.92±0.21 (10)	4.40	33.65	45.98	1:18.09	68.18	5.65	6.76
Mimusops obovata	Orange-red	35×20 mm	1.20±0.06 (10)						5.19	5.16
Peddiea africana	Purplish-black	10×7 mm		4.48	25.44	36.06	1:13.72	75.30	13.70	19.60
Podocarpus henkelii	Olive-green	25 mm diam		17.71	5.03	10.19	1:0.86	4.05		
Rauvolfia caffra	Black	15 mm diam	1.87±0.20 (10)	2.53	37.25	40.69	1:30.82	59.59	6.84	10.70
Rhamnus prinoides	Purplish-black	6 mm diam	0.25±0.02 (10)	6.33	24.52	19.55	1:6.97	81.10	10.81	6.23
Rothmannia globosa	Brown	25 mm diam		1.52	0.59	4.06	1:3.06			
Searsia rehmanniana	Yellowish	4 mm diam	0.02±0.001 (10)					78.04	9.37	2.09
Solanum gigantea	Shiny red	10 mm diam	0.24±0.02 (10)		16.76	18.84		79.91	10.28	0.73
Syzygium cordatum	Deep purple	18×9 mm	2.46±0.10 (10)						5.91	0.72
Tarenna junodii	Purplish-black	8 mm diam		0.03	0.23	0.52	1:24.63			
Trema orientalis	Black	4 mm diam	0.03±0.004 (10)	2.22	2.98	3.29	1:2.82	66.25	17.43	33.49
Tricalysia lanceolata	Black	6–8 mm diam	0.09±0.014 (10)	7.24	26.13	29.10	1:7.63	73.28	9.53	1.51
Trichilia dregeana	Brown	50 mm diam	1.48±0.04 (10)	5.02	9.81	9.44	1:3.84	41.84	10.34	36.13
Trichilia emetica	Pale brown	25 mm diam	3.07±0.15 (10)						8.37	50.22
Vitex ferruginea	Purplish-black	21 mm diam		9.24	7.86	4.81	1:1.37	44.52		
Ximenia americana	Orange	20–25 mm diam			16.47	1.72		41.18		
Xylotheca kraussiana	Yellow	40 mm		1.37	3.88	5.20	1:6.62	73.95		

Note: numbers in parentheses are sample sizes.
[a] (Griffiths and Lawes, 2006; Boon, 2010).

nitrogen content. Firstly, it was assumed that all the nitrogen of the food was present as protein, and secondly that all of the food protein contained 160 g n/kg (McDonald et al., 1995).

2.4. Analyses

A sample size of one was used for % water content, % protein content, and % lipid content. Due to missing values, only traits from 19 fruit species (Table 2) were compared using Principle Components Analysis (PCA), using STATISTICA version 7 (Statsoft, Tulsa, USA). Descriptive statistics were also used and means are presented ±1 SE.

3. Results

Out of the fruits used, *Trichilia dregeana*, *Annona senegalensis*, and *Xylotheca kraussiana* were the largest in diameter (c. 50 mm, 40 mm, and 40 mm respectively), and *A. senegalensis* and *Carissa macrocarpa* had the heaviest wet mass (including seeds) (means: 25.07±0.73 g and 14.23±1.32 g respectively) (Table 1).

Most of the fruits (84%) were hexose dominant with 50% being fructose and 34% being glucose dominant (Table 1). Only 16% of the fruit species analysed for sugar content were sucrose dominant (Table 1). Percentage water content was generally high for all fruit species (mean: 68.1±3.3%; n=30) (Table 1) and ranged from 4.1% in *Podocarpus henkelii* to 87.8% in *Ficus sur*. Percentage protein and percentage lipid content of the fruit pulp was generally low for all fruit species (mean: 8.2±0.5%; n=30 and mean: 9.3±2.2%; n=30 respectively) (Table 1). Percentage protein content ranged from 3.0 to 17.4% in *Kraussia floribunda* and *Trema orientalis* respectively; and percentage lipid content of the fruit pulp ranged from 0.6 to 50.2% in *Cordia ovalis* and *Trichilia emetica* respectively (Table 1).

Table 2
Codes for 19 indigenous tree species used in the Principle Components Analysis.

Code	Species name
AS	*Annona senegalensis*
AV	*Antidesma venosum*
AD	*Apodytes dimidiata*
BM	*Bridelia micrantha*
CI	*Canthium inerme*
CM	*Carissa macrocarpa*
CA	*Celtis africana*
CG	*Clerodendrum glabrum*
CO	*Cordia ovalis*
FN	*Ficus natalensis*
FS	*Ficus sur*
HC	*Harpephyllum caffrum*
ML	*Maesa lanceolata*
MC	*Mimusops caffra*
RC	*Rauvolfia caffra*
RP	*Rhamnus prinoides*
TO	*Trema orientalis*
TL	*Tricalysia lanceolata*
TD	*Trichilia dregeana*

The PCA analysis of fruit traits resulted in 15.27% and 10.07% of the total variance being explained by factor 1 and factor 2 respectively (Fig. 1). Sucrose (+0.04), glucose (+0.44), fructose (+0.43), and water (+0.21) were positively correlated with factor 1. Protein (−0.36) and fat (−0.41) were negatively correlated with factor 1. Sucrose (+0.60) was also positively correlated with factor 2. Glucose (−0.23), fructose (−0.08), protein (−0.31), fat (−0.16), and water (−0.21) were negatively correlated with factor 2.

4. Discussion

Out of the 38 indigenous South African fruits analysed in this study, 84% were hexose dominant and 16% sucrose dominant. Our results were similar to those of Baker et al. (1998), where most New and Old World fruits were hexose-dominant with only a small percentage of the fruits being sucrose-dominant. The PCA analysis of fruit traits showed only 15.27% and 10.07% of the total variance being explained by factor 1 and factor 2 respectively, with most fruits clustered together.

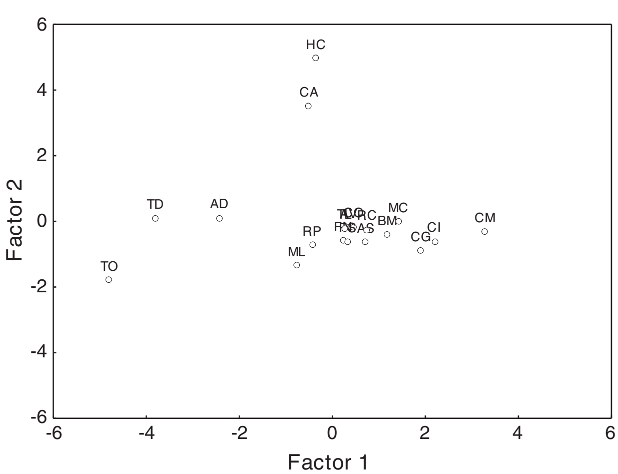

Fig. 1. Principal component analysis of 19 indigenous fruit species from KwaZulu-Natal, South Africa.

Mean percentage protein content of fruit (dry weight, 8.2±0.5%; n=30) obtained in this study was higher than those obtained in other studies that ranged from 4.6 to 7.0% (Eriksson and Ehrlén, 1991; Herrera, 1987; Izhaki, 1992; Johnson et al., 1985; Pizo, 2002; Sakai and Carpenter, 1990). However, most of these fruits are northern hemisphere species. Furthermore, controlling for phylogeny would be an important part for further comparison. Mean percentage protein and percentage lipid (dry weight, 9.3±2.2%; n=30) content in fruit in the present study were lower than those obtained by Voigt et al. (2004) for some South African indigenous fruit tree species. Voigt et al. (2004) found concentrations of c. 14% (n=26) and c. 25% (n=30) for protein and lipid content respectively. Unfortunately individual fruit species values are not presented in Voigt et al. (2004) to allow further comparison.

Mean percentage lipid content of South African fruits in the current study was lower than *Cornus racemosa* (21.3–32.5%, n=3) (Borowicz and Stephenson, 1985) but higher than *Cornus amomum* (5.4–6.6%; n=3) (Borowicz and Stephenson, 1985) fruits. Percentage lipid content for *Rhamnus prinoides* (6.2%; Table 1) was similar to that of *Rhamnus alaternus* (5.7±3.5%, mean±SD; Izhaki et al., 2002). Percentage protein content (10.8%; Table 1) for *R. prinoides* was however, much higher than *R. alaternus* (1.2±0.4%, mean±SD; Izhaki et al., 2002). Percentage water content (81.1%; Table 1) for *R. prinoides* was higher than *R. alaternus* (68.4±2.6%, mean±SD; Izhaki et al., 2002). Mean percentage water content was similar to those obtained by Borowicz and Stephenson (1985), Izhaki (1992) and Fukui (2003), who obtained percentage water content that ranged from 48.3 to 79.4%.

Only three species examined in this study for protein and lipid content have previously been studied (Table 3). Protein and lipid contents for *Mimusops obovata* (5.2% and 5.2% respectively) and *Mimusops caffra* (5.7% and 6.8% respectively) were similar to those obtained by Gaynor (1994) and Lawes (1990) respectively (Table 3). However, protein (8.5%) and lipid (2.6%) contents for *Grewia occidentalis* were lower than those obtained by Lawes (1990) with values of 14.7% and 4.4% respectively (Table 3).

Previous studies (Wellmann and Downs, 2009; Wilson and Downs, 2011a,b) have used artificial fruits to determine sugar preferences and digestive efficiencies of some South African frugivores (e.g. Cape white-eyes, *Zosterops virens*; Knysna Turacos, *Tauraco corythaix*; and Purple-crested Turacos, *Gallirex porphyreolophus*). However these fruits were made according to Witmer's (1998) artificial fruit composition that approximated the sugar concentration of North American fruit species. Our current results suggest that indigenous South African fruits have lower sugar concentrations than North American fruits (Table 1), however this trend might shift as further fruit species are sampled. Mean percentage protein

Table 3
Nutritional content of indigenous tree species.

Species	Water (%)	Protein (%)	Lipid (%)	Reference
Acacia karroo		28.10	7.20	Lawes (1990)
Acacia nigrescens		21.50	2.00	Gaynor (1994)
Bridelia cathartica		6.03	1.31	Gaynor (1994)
Calodendrum capense		14.73–15.97	37.38	Wirminghaus et al. (2002)
Capparis brassii		8.30	4.20	Gaynor (1994)
Cassine transvaalensis (*Elaeodendron transvaalense*)	80.02	10.71	3.36	Gaynor (1994)
Cladostemon kirkii		6.79	3.79	Gaynor (1994)
Diospyros inhacaensis		10.86	2.60	Lawes (1990)
Diospyros natalensis		2.73	2.07	Lawes (1990)
Dovyalis caffra		3.84	5.75	Gaynor (1994)
Dovyalis longispina		15.80	3.21	Lawes (1990)
Euclea natalensis		4.45	1.79	Lawes (1990)
Euclea shimperii (*Euclea daphnoides*)		5.03	7.00	Gaynor (1994)
Ficus glumosa	78.32	7.62	1.89	Gaynor (1994)
Ficus ingens	80.30	5.70	7.40	Gaynor (1994)
Ficus soldanella (*Ficus abutilifolia*)	75.20	13.41	14.27	Gaynor (1994)
Ficus sycamorus		5.75	9.24	Gaynor (1994)
Grewia monticola		10.37	1.51	Gaynor (1994)
Grewia occidentalis		14.65	4.44	Lawes (1990)
Mimusops caffra		6.56	7.19	Lawes (1990)
Mimusops obovata		5.45	4.52	Gaynor (1994)
Olea africana (*Olea europaea* subspecies *africana*)		4.25	3.74	Gaynor (1994)
Olea woodiana		16.96	9.20	Lawes (1990)
Podocarpus falcatus (*Afrocarpus falcatus*)	64.8 + 1.21	4.15	20.12	Wirminghaus et al. (2002)
Podocarpus henkelii		6.18–6.61	2.34–3.1	Wirminghaus et al. (2002)
Podocarpus latifolius	61.64 + 1.36	8.36–10.18	2.87–3.95	Wirminghaus et al. (2002)
Rhus natalensis (*Searsia natalensis*)		8.38	5.93	Lawes (1990)
Schutia myrtina		6.97	4.92	Lawes (1990)
Scutia myrtina		8.23–8.37	10.83	Wirminghaus et al. (2002)
Sclerocarya caffra (*Sclerocarya birrea* subspecies *caffra*)		6.90	6.60	Gaynor (1994)
Scolopia zeyheri		7.81	4.89	Lawes (1990)
Sideroxylon inerme		8.29	24.11	Gaynor (1994)
Sideroxylon inerme		10.35	9.83	Lawes (1990)
Strychnos madagascariensis		4.73	2.68	Gaynor (1994)
Strychnos madagascariensis		9.21	0.78	Lawes (1990)
Strychnos usambarensis		8.06	2.82	Gaynor (1994)
Tricalysia sonderiana		9.66	2.82	Lawes (1990)
Vangueria esculenta		3.10	1.39	Gaynor (1994)
Ziziphus mucronata	71.15	20.82	3.83	Gaynor (1994)

Note: new names according to Boon (2010) are in parentheses.

content of South African fruits in the present study was higher than that of North American fruits (3.2%, Witmer, 1996; 1998). Consequently Witmer's (1998) artificial fruit composition is not representative of what South African fruit are providing in general. However, it does fall in the range and is useful if only sugar digestion is being investigated.

Fruit colour is known to influence fruit selection by avian frugivores (Burns, 2005; Murphy, 1994; Schaefer et al., 2008). Of the fruits examined in this study 29% were black and 43% were red when ripe (Table 1). It has been suggested that the colour of ripe fruit has co-evolved with colour vision in birds (Osorio and Vorobyev, 1996).

It is generally assumed that large frugivores can disperse a wider range of fruit and seed sizes than smaller frugivores, however, avian frugivores process fruits in different ways (Levey, 1987). Gulpers ingest fruits whole, while mashers crush the fruit first and then ingest the pulp only (Levey, 1987). In both of these gape width is a limiting factor (Jordano, 2000; Martin, 1985; Wheelwright, 1985). Indeed, Avery et al. (1993) found that handling time (defined as the time from picking up a food item to the time of ingestion; Hedge et al., 1991) increased as fruit size increased. They suggest that avian frugivores should prefer the largest fruit possible that they can ingest without incurring handling costs.

Fruit width in this study ranged from 4 mm (*Searsia rehmanniana* and *T. orientalis*) to 40 mm (*A. senegalensis*, *F. sur* and *X. kraussiana*) (Table 1). In Africa, avian frugivores play a more important role in seed dispersal than primates (Bleher and Böhning-Gaese, 2001; Holbrook and Smith, 2000). Studies on the gape width of South African avian frugivores are limited but Knysna (*T. corythaix*) (c. 310 g) and Purple-crested (*G. porphyreolophus*) Turacos (c. 300 g) (Du Plessis and Dean, 2005a, b) have gape widths of 25 mm and 15 mm respectively (Wilson and Downs, unpublished data). Besides for some hornbill species, such as the Trumpeter Hornbill (*Bycanistes bucinator*) (567–721 g) (Kemp, 1995; Sanft, 1960), Knysna and Purple-crested Turacos are two of the largest South African avian forest frugivores (Du Plessis and Dean, 2005a, b).

Potentially 16% and 47% of the fruits respectively examined in this study (Table 1) are too large to be ingested whole by these two species as both swallow their fruit whole (pers. obs.). Although some other bird species will peck at larger fruits and ingest seeds in this way (Voigt et al., 2004). Both these Turaco species are forest inhabitants (Du Plessis and Dean, 2005a,b) and are therefore threatened by forest fragmentation (Lawes et al., 2000; Low and Rebello, 1996). It is important that management plans for forest conservation are developed in order to protect plant–animal interactions in forest ecosystems in the long-term (Kankam and Oduro, 2009; Kirika et al., 2008).

In conclusion, fruits are generally considered as being either nutrient-dilute or nutrient-dense (Izhaki, 1993). Fruits in this study were generally observed to be high (>50%) in water content (except for *P. henkelii*), and low (<10%) in protein and lipid content indicating that these fruit species could be considered as nutrient-dilute. Avian frugivores would therefore need to consume large amounts of these fruit species in order to obtain sufficient energy (Worthington, 1989). However, it should be noted that absolute concentrations of sugar, protein and lipids may be different for different seasons and locations and may vary due the physiological condition and age of the tree.

Future studies need to determine the nutritional composition of the remaining indigenous South African fruits as well as examine non-nutritive factors (e.g. fruit colour, seed-to-pulp ratio, seed size, fruit size, secondary compounds, micro-nutrients etc.) in order to develop a comprehensive database.

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